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ORGANIZATION OF PRIMITIVE NERVOUS SYSTEMS. NEUROMUSCULAR PHYSIOLOGY OF *GYROCOTYLE URNA*, A PARASITIC FLATWORM

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The free-living flatworms are usually considered to occupy a strategic position at the base of the metazoan phylogenetic tree. They are the first bilaterally symmetrical animals to possess a brain concommitant with the concentration of neural tissue into discrete nerves. The nervous system itself is of interest because it probably reflects various aspects of the primitive conditions which existed during the evolution of centralization. In a number of species, for example, the anatomical arrangement of nerve cells appears to be intermediate in organization between the diffuse nerve-nets of many coelenterates and the more highly concentrated systems of higher protostomes (Koopowitz, in preparation). Neuromuscular preparations among the free-living flatworms have only been reported from polyclad turbellarians (Gruber and Ewer, 1962; Koopowitz and Ewer, 1970). This scarcity of information reflects the general unsuitability of these animals as neurophysiological preparations. Not only does their acoelous nature preclude easy exposure of nerves but their fragility makes it almost impossible to restrain them for any but the shortest lengths of time. The latter problem can be avoided by using parasitic flatworms which have a tough outer cuticle. However, except for some early mechanical recordings of drug effects on *Fasciola*, the liver fluke (Chance and Mansour, 1949; Mansour, 1957), no neurophysiological investigations appear to have been reported for either trematode or cestode parasites.

The report that follows is a preliminary investigation on the neuromuscular properties and capabilities of preparations made from a cestodarian flatworm, *Gyrocotyle urna*. Cestodarian flatworms are an unusual group of unsegmented animals which are classically placed in a sub-class of the Cestoda, the parasitic tapeworms (Barnes, 1968). Modern workers now consider them an aberrant group, not closely related to present day tapeworms but rather remnants of a stock closer to the original primitive parasitic platyhelminths (Burt, 1970; Wardel and McLeod, 1952). These unique animals have a nervous system reduced to a pair of longitudinal cords with commissures at each end and a posterior nerve ring. The neuronal anatomy appears much simpler than that found in either the polyclads or the freshwater planarians. Besides shedding light on the nervous organization of primitive flatworms, these animals should reflect those adaptations produced to meet an endoparasitic existence. Specific neuromuscular adaptations to parasitic modes of life have so far received little attention.

Methods and Materials

Gyrocotyle urna is found close to the spiral valve in the stomach of *Hydrolagus colliei*, a chimerid fish abundant in the waters of Puget Sound. The fish were

kept in large tanks of circulating sea water at the Friday Harbor Laboratories and flatworms were dissected free as needed. Virtually every fish harbors at least one of these parasites. The animals used ranged from 2 to 6 cm in length and up to 3 cm in width. Isolated flatworms will live for three to four days in cold sea water but the animals were usually used within 24 hours of extraction.

A number of different preparations were made. Most frequently the animal was sliced down its mid-line, any eggs washed out of the uterus and both anterior and posterior ends cut off. The latter operations effectively removed commissures and ganglia. This was verified by inspection. Tiny hooks made from minute pins were inserted into both ends of the preparation. One of these was fastened to the bottom of the container while the other was connected by a length of nylon floss to a mechanoelectrical transducer. Either of two transducers were used: a Brush metripak angular position transducer was utilized for isotonic contractions while a Statham "Gold Cell" was available for isometric measurements. The output from the transducers was displayed on either a Bausch & Lomb VOM6 single-channel chart recorder or on a Clevite Brush Mark 220 two-channel chart recorder.

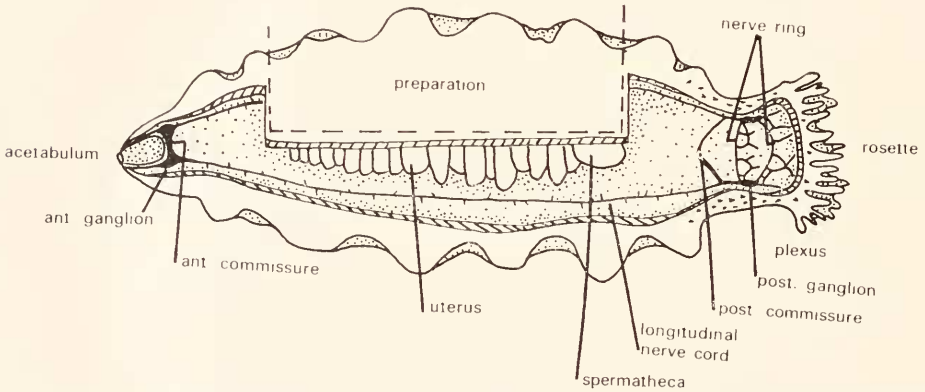

FIGURE 1. The major parts of the nervous system of *Gyrocotyle urna* as seen by dissection. The part used as the preparation was that bounded by the dashed line. This specimen was 3 cm long.

Stimuli were delivered by a pair of silver electrodes. These were insulated in polyethylene tubing sleeves except for their tips which were chlorided and flattened. The electrodes were pushd into the tissue, one electrode on each side of the longitudinal nerve trunk. A Grass S48 stimulator provided positive going square wave pulses. The preparation was suspended in 15–17° C aerated sea water which was changed every half hour.

RESULTS

Anatomy

Figure 1 shows the major nerves; these can be dissected fairly easily. There are two main nerve strands running along the length of the animal. At the anterior end they are joined by a commissure behind the muscular acetabulum. Slight swellings on either side of the commissure have been called ganglia (Watson,

1911). Along their length the major cords give off small nerves which sink into the musculature. In the central two-thirds of the animal, most of this musculature appears to be orientated longitudinally. At the posterior end there is a nerve ring which sends off branches into the funnel shaped sucker. These branches anastomose to form a small plexus. At the level of the ring the longitudinal cords form another pair of ganglionic swellings. Anterior to the ring can also be found a commissure joining the two rings. Giant cells (Watson, 1911) have been reported but, with vital methylene blue staining, they could not be found. Vital staining also showed very few somata in the ganglia. Methylene blue staining, however, is notoriously erratic. Monopolar cells were found in the longitudinal cords. A peripheral nervous system has been described (Watson, 1911) but this was not visible with a dissecting microscope.

Neuromuscular responses

A single stimulus pulse, of above threshold amplitude, results in a smooth contraction followed by a series of secondary contractions. The initial response tends to be quite slow and usually requires more than one second to reach peak tension. Even if secondary activity is not generated the time taken to relax back to the original level of tone is very long, typically more than 40 seconds. The rate of tension generation is dependent on both the intensity (Fig. 2a) and duration (Fig. 2b) of the electrical stimulus. Likewise, the total shortening of the preparation is also dependent on both intensity (Fig. 2c) and duration (Fig. 2d) of the stimulus. These responses do not bear a simple relationship to the amount of current in the stimulus. In Figure 2d the response to a 10 V stimulus of 30 msec duration is less than that to a 20 V, 10 msec shock, although the former stimulus should have greater amperage. When the total amount of current is kept constant (intensity $\times$ duration = constant) increasing the duration does not lead to larger response amplitudes but increasing the stimulus intensity does (Figs. 2e and 2f).

The threshold voltages often appear to be quite high, *e.g.,* 20 volts and 2 msec duration. This is also true of the polyclad, *Planocera* (personal observations). To see if these high thresholds could be due to some artifact, I tested the experimental situation by substituting a fragment of the nemertean *Paranemertes peregina* for the *Gytrocotyle* preparation and found threshold values for this animal closer to the expected range, *i.e.,* 4 volts and 0.3 msec duration. High threshold values may, therefore, be characteristic of platyhelminth preparations.

Inhibitory responses

In many cases, it was noticed that stimuli of intensities slightly below the threshold values for contractions caused very small decreases in the tone of the preparation. Much larger decreases in tone could be obtained if the preparation was already in a state of contraction (Fig. 3a). This case much resembles the "direct inhibition" previously described in *Planocera* (Koopowitz and Ewer, 1970). If a train of stimuli are delivered, then the initial contraction is often followed by a drop in the level of tone and a depression of spontaneous activity (Fig. 3b). After stimulation the depression is followed by a rebound in tone, as well as increases in frequency and amplitude of the spontaneous contractions. In another preparation

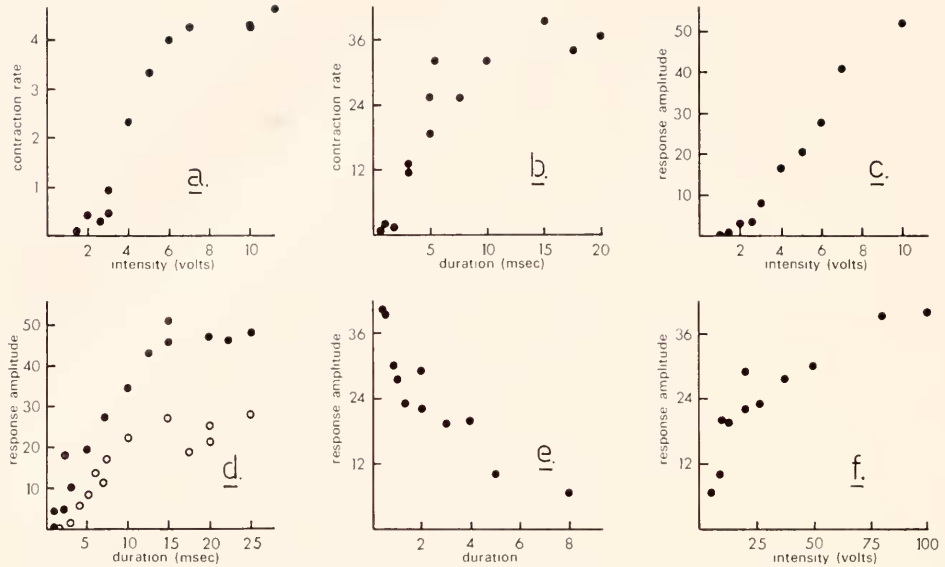

FIGURE 2. (a) Effects of stimulus intensity on rate of contraction; the axis measures the relative rate of contraction as the slope of the rising part of the trace. The abcissa measures intensity in volts. The stimulus duration was kept constant at 1.0 msec. In this, as in all other graphs, each point represents a single reading. For any graph the points are all from a single preparation. (b) Effect of stimulus duration on the rate of contraction; the axis is relative rate of contraction while the abscissa reads stimulus duration in msec. Stimulus intensity was 20 V. (c) Amount of shortening and intensity of the stimulus; axis is the relative height of the response and the abcissa the stimulus intensity in volts. Stimulus duration was held at 1 msec. (d) Amount of contraction with different stimulus durations; axis is the relative amount of shortening and the abscissa the stimulus duration in msec. Solid circles were obtained with an intensity of 20 V while the rings were obtained with an intensity of 10 V. Both were from the same preparation. (e) Amplitude of the response with changing intensity and current kept constant ($v \times d = 40$); axis is relative amount of shortening and abscissa is msec duration. (f) Amplitude of response with changing stimulus duration, current kept constant ($v \times d = 40$); abscissa intensity in volts. Same experiment as in Figure 2e.

(Fig. 3c) which was not spontaneously active, the lowered level of tone was held for 20 sec after the stimulus and the rebound contained two contractions which resembled spontaneous contractions. When the frequency and number of stimuli was increased (Fig. 3d) even more of these contractions followed. It should be noted that multiple stimuli are not necessary to elicit both contraction and relaxation, for a single stimulus can also do this (Fig. 3e) in a favorable preparation. Although cessation of spontaneous activity most likely involves an active inhibitory system, the measured "loss" in tone could also be due to contractions evoked in antagonistic muscle layers. However, the rebound following loss of tone argues against this explanation.

The amount of tension generated is also dependent upon the previous stimulation history of the preparation. Generally, the smaller the interstimulus interval the less the amount of tension generated for identical stimuli. This generalization will be qualified shortly. Figure 4a shows the response by a preparation following

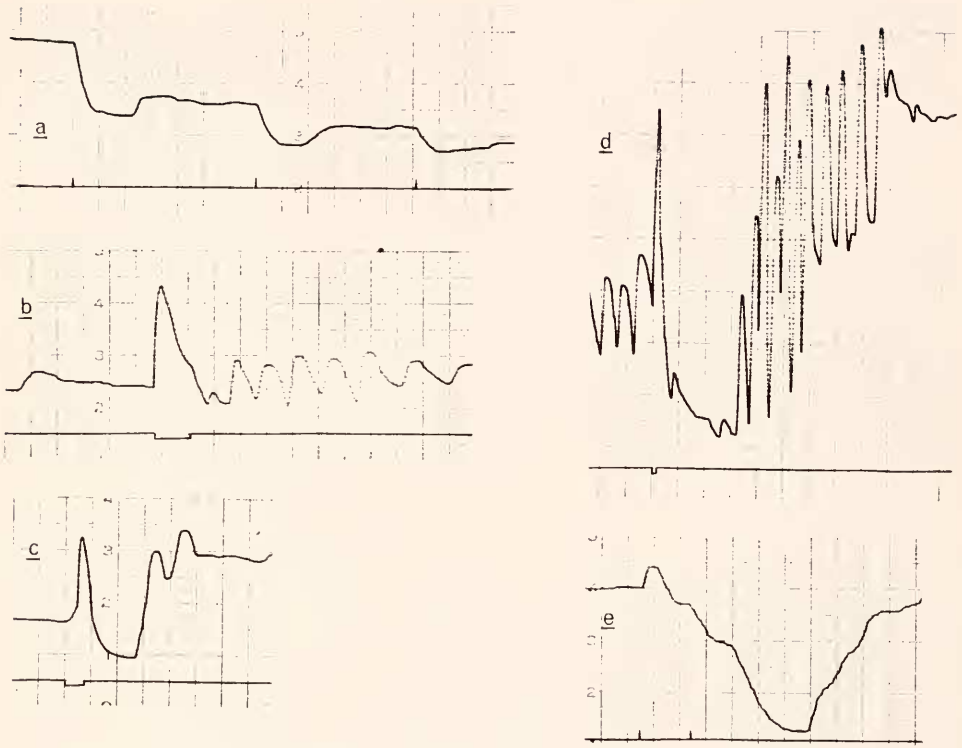

FIGURE 3. Inhibitory effects of stimuli on the level of tone; (a) the effects of three single stimuli each 40 V and 0.5 msec duration; (b) the same preparation as Figure 3c, where the stimulus train was 20 sec long with a frequency of 20 per sec. Intensity was 40 V with 1 msec duration. (c) The effects of a stimulus train 10 sec long; each stimulus was 40 V and of 1 msec duration. Frequency was 5 per sec. (d) Response to a train of stimuli 10 sec; (e) response to two stimuli four sec apart, intensity was 20 V and duration 1 msec.

three different interstimulus intervals. The recovery time for this depression varies from preparation to preparation. It usually lasts for no more than ten to fifteen minutes, although in some cases it was present for a considerably longer period. Response amplitude is plotted against interstimulus interval in Figure 4b. This decreased responsiveness could be due to fatigue in the muscle, failure of the nerve or neuromuscular junction, or some "active" process such as a long lasting inhibitory effect. It is unlikely that fatigue can account for the changes measured as they are evident in very fresh preparations. Depression can also be recorded from preparations using weak stimuli, before increasing the stimulus strength and eliciting very large responses. It is also unlikely that failure or fatigue in the nervous part of the preparation can be responsible because stimuli delivered with interstimulus intervals less than four seconds apart show facilitation.

Facilitatory responses

The contraction recorded from a second stimulus, administered within one or two seconds of the first, often results in an increase in response over that from the

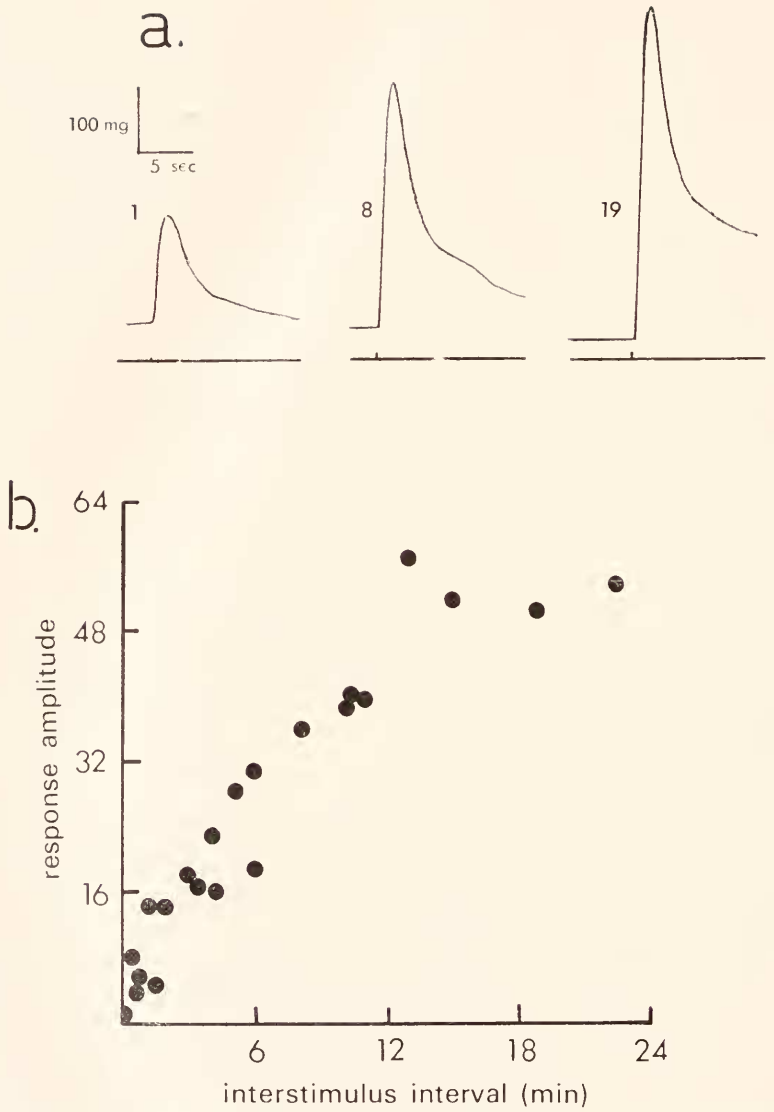

FIGURE 4. (a) Effects of interstimulus interval on the size of the response; stimuli were 30 V and 0.3 msec duration. The number next to each response was the length of the interstimulus interval in minutes. (b) Effects of interstimulus interval on the amplitude of the response; axis is the relative amount of shortening and abscissa the interstimulus interval in minutes. All stimuli were 30 V and 0.1 msec duration.

initial stimulus. Because of the slow nature of the response the facilitation is displayed as increased "treppe" step size. Response amplitude to three single stimuli of 10 msec duration is greater than the response to a 30 msec stimulus of the same intensity and the response to the second or third stimulus is greater than

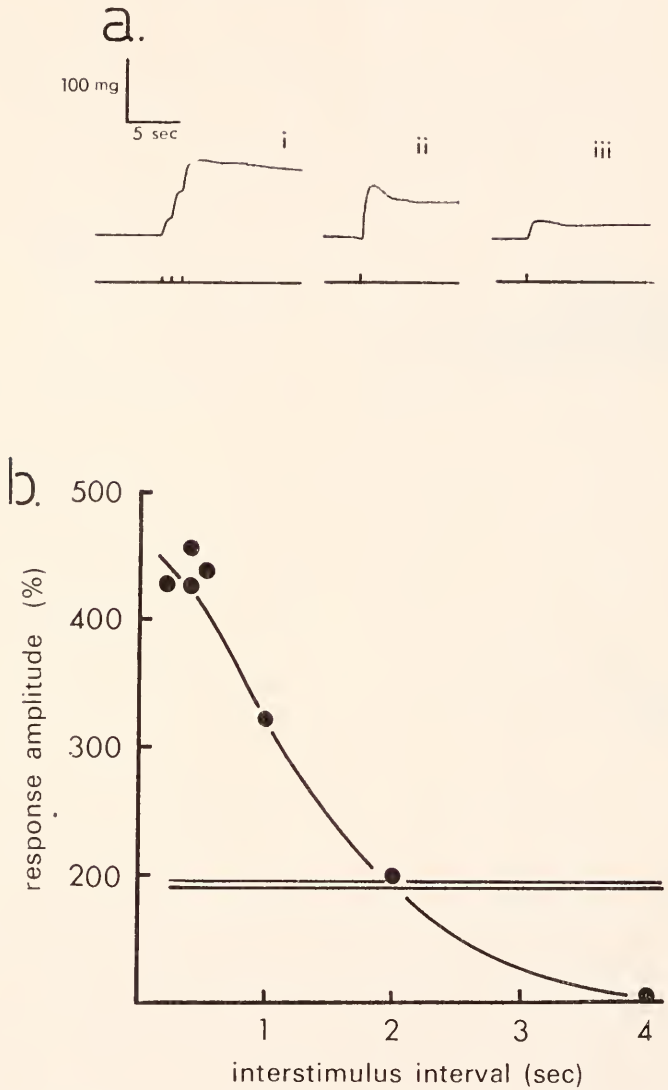

FIGURE 5. (a) Facilitatory effects. Each stimulus had an amplitude of 10 V. In i 3 stimuli of 1 msec duration were delivered at 1 sec intervals, and ii shows the response to a single shock of 3 msec duration while iii is the response to a single stimulus of 1 msec. (b) Changes in amplitude of the response with changing intervals between two stimuli; the axis is the amplitude of the response to the second stimulus expressed as a percentage of the first stimulus amplitude, while the abscissa represents the interstimulus interval in seconds. All stimuli had an intensity of 10 V and a duration of 1 msec. The double line is the response amplitude to a single shock of 10 V and 2 msec duration.

the first (Fig. 5a). In some preparations it was possible to confuse the second stimulus response with secondary activity elicited by the first stimulus especially if these were superimposed on each other. Special care was taken to avoid using

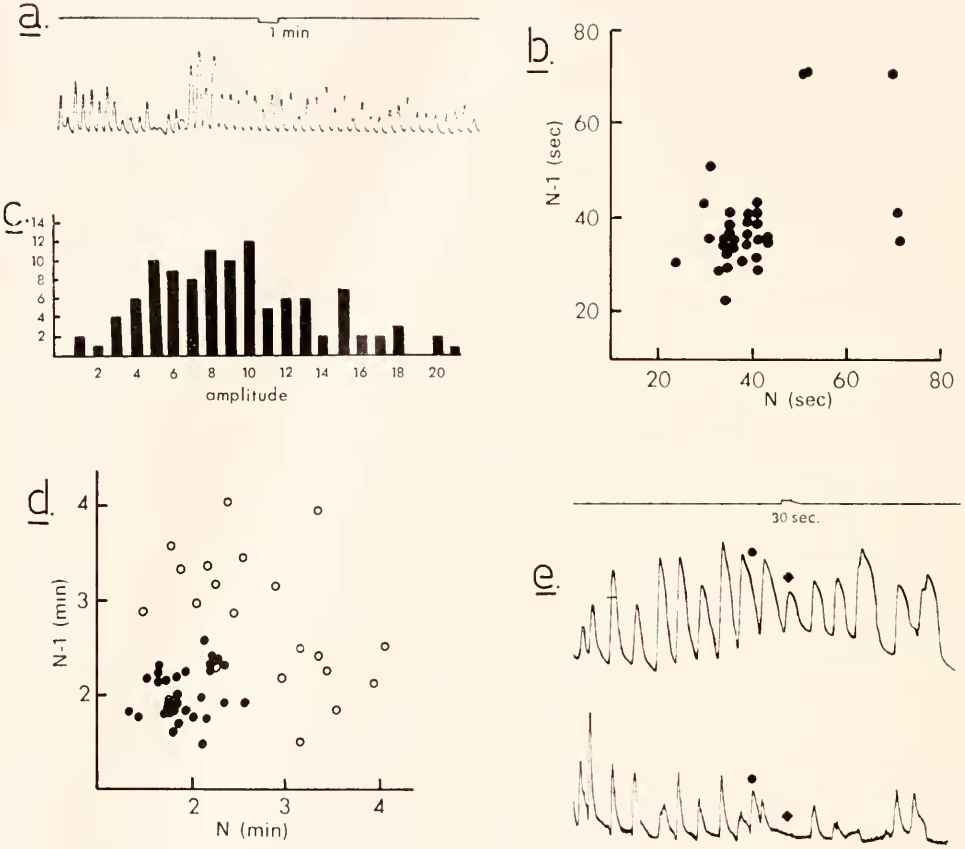

FIGURE 6. (a) Spontaneous activity from a *Gyrocotyle* preparation; (b) a joint interval histogram of the spontaneous activity. The axis is the time interval preceding a spontaneous contraction and the abscissa is the interval following the activity. Intervals are expressed in seconds. (c) Distribution of spontaneous contraction amplitudes; the frequency of occurrence is on the axis and the abscissa represents contraction amplitude or tension. This is from the same preparation in Figure 6(a) but collected for a 65-minute period. (d) Joint interval histogram for the two sides of a hemisected animal; this animal had the posterior commissure intact and the open and closed circles represent the different sides of the preparation. Intervals are expressed in minutes.

this kind of data which might be ambiguous. The time course for facilitation in one preparation is shown in Figure 5b. Here the amplitude of the second response reached a maximum when the pulses were less than 1/2 seconds apart. By the time the interstimulus interval reached 4 seconds, the responses were of equal size. It should be noted that the maximum facilitated response was more than twice the size of the response elicited by a single stimulus of the same amplitude but with twice the duration, suggesting that neuromuscular facilitation does take place. This is the first demonstration of this phenomenon in the flatworms.

Spontaneous activity

About half of the preparations set up show spontaneous contractions (Fig. 6a). The mean interval between contractions varies with the preparation and ranges from less than 20 seconds to more than 4 minutes. Figure 6b displays one preparation for which the intercontraction intervals are plotted against the preceding interval to form a joint interval histogram. The tight clustering of points indicates a fairly constant rhythm though there is some scatter and irregularity. Although the contractions tend to be more-or-less rhythmical, amplitude of contraction is quite variable (Fig. 6c). The site of origin for this activity could be either the nervous system or the muscles. Special preparations were made by removing the anterior commissure and splitting the animal halfway down the midline towards the posterior end; thus, muscular activity could be recorded from both halves of the animal simultaneously. The joint interval histogram from one such preparation (Fig. 6d) indicates that each side contains its own pacemaker system as the rhythms of the two sides are quite different. One is regular while the other tends to have short intervals followed by long. Recordings from the two sides were attempted when the anterior commissure was intact but the posterior one had been removed. Spontaneous activity was only recorded in one such preparation (Fig. 6e). Here the spontaneous activity in both sides of the animal was sychronized and matched except for two contractions. Unfortunately the activity died away before the anterior commissure could be severed. Nevertheless, data presented in the next section suggest that the anterior and not the posterior commissures are involved with coordination of longitudinal muscle activity between the two sides of the animal; thus the synchronization between the two sides displayed in Figure 6e may be of some significance.

Coordination between the two sides

When, as above, partially hemisected preparations are set up, with the anterior commissure intact, then stimulation of one side will set up contractions in both halves. If the commissure is severed, however, then only the directly stimulated side of the preparation will contract. A similar set of experiments was conducted to determine whether transmission also took place across the posterior commissure or ring. In only one preparation out of six did I find transmission through the posterior portion of the animal. The transmitted response was quite different from that usually obtained with anterior conduction. The latency ranged from 2 to 7 seconds compared with less than one second for transmission involving the acetabular commissure; the transmitted response in the posterior conducting system also appears to lack the rapid component seen with anterior transmission. Without more data, however, it is difficult to decide whether or not posterior transmission is of any significance.

Discussion

A neuromuscular explanation for the reported observations is desirable, however, without intracellular records from the nerves and muscle cells themselves, any hypotheses must remain rather tenuous. This system has rather slow contraction rates and even longer times for return to resting tension levels. Both short term

facilitation and a longer lasting inhibition have also been described and spontaneous activity in the animal tends to be in the form of more-or-less rythmical contractions. At first glance *Gyrocotyle* appears to share many of the properties of coelenterate anthozoan preparations. This should not be taken as an indication of phylogenetic closeness as the free-living polyclad *Planocera*, investigated by Gruber and Ewer (1963), shows few similarities to coelenterate neuromuscular systems. Also, the extent to which the *Gyrocotyle* neuromuscular system reflects the parasitic nature of the organism is not clear but there are some surprizing similarities with the unrelated nematode *Ascaris*.

Comparing neuromuscular properties of *Gyrocotyle* with those of *Planocera*, a polyclad flatworm (Gruber and Ewer, 1962; Koopowitz and Ewer, 1970), reveals a number of both similarities and differences. The major difference concerns neuromuscular facilitation. Facilitation, a common property of many invertebrate neuromuscular preparations, cannot be clearly demonstrated in the free-living worms. *Gyrocotyle*, however, does show facilitation. The absence of the phenomenon in polyclads may, therefore, be a peculiarity of that species rather than indicative of a condition in the entire phylum. Nevertheless, even in *Gyrocotyle*, facilitation is difficult to evince unless one has a particularly favorable preparation. In most cases the muscular response to a second stimulus is markedly less than the response to a first stimulus. This antifacilitation occurs even when contractions are elicited by small amplitude stimuli which result in responses that are a tiny fraction of the possible tetanus tension. Similar stimuli are needed to demonstrate facilitation in favorable preparations. The facilitatory effects of a stimulus are short and usually last on the order of seconds (Fig. 5b) in contrast to the depression which may last for a considerable time (Fig. 4b), usually tens of minutes.

The time course for facilitation in *Calliactis* (Pantin, 1935) and *Cerianthus* (Horridge, 1958), both sea-anemones, peaks between 0.1 and 0.2 sec and then rapidly falls away within a few seconds. Maximum facilitation in *Metridium* occurs at stimulus intervals of 0.5 sec (Robson and Josephson, 1969). In a tropical species of *Calliactis* Josephson (1966) found that facilitation only lasted for 0.6 seconds. On the other hand Arai (1965) recorded facilitatory effects that lasted as long as 8 min in *Pachycerianthus*. Except for the latter case these values are similar to those obtained with *Gyrocotyle*. Comparatively little is known of inhibitory systems in coelenterates but evidence suggests that in *Calliactis* inhibition may be prolonged (Ewer, 1960) and much longer lasting than the facilitatory events. Intracellular recording from *Ascaris* (del Castillo *et al.*, 1967) suggests that in the somatic musculature facilitatory events are ephemeral compared to inhibitory. The later event being more easy to evoke. They found, however, that records of "synaptic" transients showed similar time courses for both depolarizations and hyperpolarizations. Multiple stimuli, however, lead to prolonged periods of hyperpolarization. Whether these longer inhibitory effects are due merely to the amount of transmitter released or active post-junctional membrane changes has not been ascertained.

Another difference between *Planocera* and *Gyrocotyle* resides in the inhibitory systems. The inhibitory thresholds in the polyclad are much higher than the excitatory. In *Gyrocotyle*, however, direct muscle relaxation can often be obtained

by stimuli of intensities below those used to make the preparation contract. Other properties of the depression systems appear to be quite similar. Both preparations have similar time courses for the long-term inhibitory decay following stimulation and in both animals inhibitory phenomena can be produced by multiple stimuli where a single stimulus is ineffective. This suggests that some sort of inhibitory facilitation may exist. The data displayed in Figure 3b and Figure 3c are of interest as they show that a period of inhibition can be followed by a period of rhythmical contractions and that the number of contractions may be related to the amount of inhibition. The longer the stimulus train the greater the number of contractions. If, as it appears, this activity involves some sort of a rebound from an inhibitory state then it more likely involves short term rather than long term inhibitory systems. Long term depression normally lasts for many minutes; during these experiments, the tone of the preparation was depressed for a much shorter time period than would have been expected.

With comparable stimuli, both *Gyrocotyle* and *Planocera* (Koopowitz, unpublished observations), require approximately the same length of time to reach peak tension during a twitch. This is quite a slow process and usually takes between 0.5 and 1.0 seconds. Polyclad muscle, however, relaxes in less than 10 seconds, whereas the cestodarian usually requires at least 40 seconds. The longer time course for *Gyrocotyle* appears to involve an "active" component because the tension measured during relaxation is similar whether isotonic or isometric transducers are used. If the slow relaxation was due merely to inelastic properties resisting stretch, one might expect different time courses for relaxation with the different transducers. Further investigation is needed to discover exactly what physiological properties of the system determine the speed of relaxation.

In *Ascaris,* esophageal muscle cell tension appears to be maintained as long as the muscle cell remains depolarized (del Castillo and Morales, 1967) and in fact relaxation can be elicited more rapidly with hyperpolarizing potentials. Whether this is the case in *Gyrocotyle* is not known. Relaxation times for sea-anemones are much slower than the worms but direct comparisons are difficult as multiple stimuli are usually used to evoke activity in anemone preparations. Both *Cerianthus* (Horridge, 1958) and *Pachycerianthus* (Arai, 1965) will produce twitches to single stimuli and here relaxation is much longer than in *Gyrocotyle.* Muscle action potentials measured from *Calliactis* appear to be transient and muscle cell depolarization cannot account for the maintained tonus (Josephson, 1966).

In anemones, two kinds of muscular activity have been reported, twitches and slow contractions. The latter have been difficult to investigate and their nature is unclear (Robson and Josephson, 1969; Ross, 1957). Slow responses were often obtained following evoked twitches and in this way resemble the secondary activity recorded from *Gyrocotyle.* The complex nature of secondary activity and the repetition of the contractions suggest some kind of reverberating activity might exist. Josephson (1966) found that single stimuli could evoke multiple firing in *Calliactis* and this effect, but on a larger scale, could be involved with flatworm secondary activity.

So little is known of the behavioral repertoire and adaptations to an endoparasitic existence that it would be profitable to discuss some aspects of behavior which have been observed with *Gyrocotyle.* Interactions between adjacent animals

occur. On one occasion when a host was opened and two worms were found, one of the animals had attached quite firmly to the other with its acetabulum. Animals lying next to one another in a dish of sea water have been observed to grip each other with their acetabulum. This behavior has also been observed in some free-living polyclads, *e.g., Enchiridium punctatum* (Koopowitz, unpublished observation). It is not clear whether this is part of a prelude to copulation. The acetubulum of *Gyrocotyle* tends to be used in an exploratory manner; when an animal is first introduced into a container of sea water this structure is extended and moved in a number of directions. There is the impression of a sensory structure being used to sample the environment. In another set of chance observations, a young worm was seen to emerge from the genital aperture of a large adult. Most of the young worm's activity during the "birth" seemed to involve its own acetabulum. When the small worm was free, it started to undulate in the nearest approach to locomotory activity that has been seen. A number of waves of dorsoventral flexions passed down the animal's body, rather reminiscent of polyclad swimming, and the animal moved with the acetabulum leading. These observations suggest that the acetabular tip is the anterior end of the animal.

There was an old controversy about the scolex in tapeworms and whether this represented the anterior or the posterior end of the animal. Considerable evidence has been accumulated that the scolex is the anterior end (Wardle and McLeod, 1952) and the problem now appears to be settled. However, the rosette holdfast of *Gyrocotyle* is usually considered to be homologous with the scolex of the *Eucestoda* (Wardle and McLeod, 1952). This paradox is most easily resolved if one considers the *Gyrocotyle* holdfast to be only functionally analogous to the scolex. This may well be the case if, in fact, the two kinds of animals are not closely related.

One of the outstanding features of *Gyrocotyle* is the apparent simplicity of the nervous system and the ease with which it may be exposed for experimental manipulation. Experiments reported here, while not expressly designed to investigate purely neuronal interactions, do give some insight into the organization of the nervous system. It is probable that the pacemakers for spontaneous longitudinal contractions occur in the main longitudinal nerve trunks as this was the main nervous tissue in the preparations. Each side has at least one pacemaker system and synchronization takes place across the anterior commissure. Stimuli from one side of the body are also able to cross to the other side via this commissure. The acetabular commissure then possesses properties similar to those demonstrated in polyclad brains (Gruber and Ewer, 1962). It is tempting to consider the commissure and its "ganglia" as homologues of the early flatworm brain. More intriguing is the possibility that we are dealing with a brain that is still both at a very primitive stage and involved with the initial functions for which brains were evolved. This flatworm is now accepted to be derived from the stock which originally gave rise to the other parasitic platyhelminths (Burt, 1970). The association of primitive parasites with primitive hosts is often exemplified by *Gyrocotyle* and its chimerid host. The ganglia and commissure could, on the other hand, represent a secondarily reduced brain. The animal's parasitic habit, which presumably has resulted in a reduced need for it to interact with its environment, may have left it with only the essential neuronal circuitry necessary to deal

with these limited needs. A careful inventory of the functions and physiology of this "brain" might be expected to throw considerable light on the factors underlying brain evolution.

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Summary

1. The nervous system consists of two longitudinal nerve cords with commissures at each end. Ganglia are reduced to small swellings in the cords adjacent to the commissures. At the posterior end there is a nerve ring with a reduced nerve plexus in the rosette.

2. The responses to electrical stimulation are described. Preparations have high thresholds and relatively slow twitch contractions.

3. Direct stimulation often causes loss of muscular tone. This and decreased responsiveness to repeated stimulation are thought to be due to the presence of inhibitory neurones.

4. Facilitation of the response to electrical stimulation is short lasting. This effect has usually decayed within a few seconds of stimulation.

5. Rhythmical spontaneous contractions occur. Pacemakers for this activity are probably in the longitudinal nerve trunks.

6. The anterior acetabular commissure is used to synchronize the spontaneous activity of the two sides. Electrical stimuli applied to one side will cause the other to contract if the anterior commissure is intact.

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